

HAWK OWLS IN FENNOSCANDIA: POPULATION FLUCTUATIONS, EFFECTS OF MODERN FORESTRY, AND RECOMMENDATIONS ON IMPROVING FORAGING HABITATS

GEIR A. SONERUD

*Department of Biology and Nature Conservation, Agricultural University of Norway,
P.O. Box 5014, N-1432 Ås, Norway*

ABSTRACT.—Hawk Owls (*Surnia ulula*) are diurnal raptors found across the northern hemisphere in open boreal forest habitats. In Fennoscandia (Finland, Sweden and Norway), their diet consists mainly of microtine rodents. The population densities of these microtines usually peak every 3–4 yr and fluctuations are geographically asynchronous. Hawk Owls respond by concentrating and breeding where and when microtine abundance is high. The resulting strong temporal and spatial short-term variation in Hawk Owl density in Fennoscandia makes any long-term population trends difficult to detect. Hawk Owls locate their prey visually from elevated perches and need ample space for long-range scanning and attack. Therefore, harvesting old forest by clear-cutting is believed to benefit the Hawk Owl. However, this may depend on the values of several variables, such as clear-cut size and shape, height of trees in clear-cut edges, density and height of residual trees left in clear-cuts after logging, type and extent of ground cover and prey species composition and abundance in clear-cuts compared to old forest. Based on data on the Hawk Owl's attack range, recommendations are made for spacing of residual trees as hunting perches. No single habitat in Fennoscandian forests seems to be superior for foraging Hawk Owls throughout the year and the effects of modern forestry on Hawk Owls, although probably positive, at present are difficult to predict.

KEY WORDS: *Foraging, forestry, habitat, Hawk Owl, management, Surnia ulula.*

Búho Halcón en Fennoscandia: fluctuaciones de poblaciones, efectos de forestal moderno, y recomendaciones en mejorando hábitat de forraje

RESUMEN.—El Búho Halcón *Surnia ulula* son rapaces del día encontrados a través del hemisferio norteño en hábitat abierto en bosques boreal. En Fennoscandia (Finland, Sweden y Norway), su dieta consiste por mayor de "roedor microtine." La población densidad de estos "microtines" normalmente llega su mas alto cada 3–4 años, y fluctuaciones son geográficamente sincronizados. Búho Halcón responde en concentraciones y criando donde y cuando abundancia de "microtine" esta alto. El resultado del temporal fuerte y variación especie de corto tiempo en la densidad del Búho Halcón en Fennoscandia hace cualquier tendencia de duración larga de población difícil a descubrir. Búho Halcón localiza su cazado visualmente en percha elevada, y necesitan espacio amplio para visualizar de larga distancia y ataque. Por eso, cosechas de bosques viejos con cortadas-completas es creído dar beneficios al Búho Halcón. Sin embargo, esto puede depender en el valor de varios variables, como el tamaño de corto-completo y forma, altura de árbol en orillas de corte-completo, densidad y altura de árboles residuales dejados en áreas de cortes completos después de la cosecha, tipo y extenso de terreno, composición y abundancia de especie de cazar en cortes completos comparado a bosques viejos. Basado en los datos del alcance de ataque del Búho Halcón, recomendaciones están hechas para el espacio de árboles residuales como perchas de cazar. Ningún hábitat singular en bosque de Fennoscandia, parece ser superior para el forraje del Búho Halcón a través de todo el año, y los efectos de forestales moderno en los Búho Halcón, aunque problemamente positivo, en el presente es difícil pronosticar.

[Traducción de Raúl De La Garza, Jr.]

Hawk Owls (*Surnia ulula*) are medium-sized (body mass about 0.3 kg) diurnal raptors which range across the northern hemisphere in open boreal forest habitats (Glutz von Blotzheim and

Bauer 1980, Cramp 1985, Norberg 1987). In the western Palearctic region their diet consists almost exclusively of small mammals, mainly microtine rodents (Mikkola 1983, Cramp 1985, Hogstad 1986,

Sonerud 1986), which they locate visually from elevated perches (Sonerud 1980, 1992).

In Fennoscandia (Finland, Sweden and Norway), the original role of fire and storms as the major disturbance agents in the boreal forest (see Zackrisson 1977) has been gradually superseded by humans during recent centuries. During the past 30–40 yr, modern forestry has transformed most of the semipristine and continuous forest, shaped by selective harvesting of the largest trees, into a mosaic of patches interspersed with clear-cuts and plantations (see Rolstad and Wegge 1989). This transformation may affect Hawk Owls in three major ways. First, Hawk Owls mostly use cavities or broken tops of snags for nesting (Cramp 1985) and may therefore experience more limited breeding opportunities in modern forests with fewer old trees as nesting sites. Second, Hawk Owls locate prey by sight (Norberg 1977, 1978, Sonerud 1986) and find suitable conditions in open habitats created by clear-cutting, where long-range scanning for and attack of ground-dwelling small mammals is enhanced. However, Hawk Owls also require elevated perches from which they search for prey (Sonerud 1980) and such perches are often lacking in clear-cuts. Third, clear-cuts support greater populations of voles than are found in old forest, especially populations of the *Microtus* voles (Henttonen et al. 1977, Larsson and Hansson 1977, Hansson 1978), although the availability of these voles may be low for much of the year (Sonerud 1980, 1986, Nybo and Sonerud 1990, Jacobsen and Sonerud 1993).

In this paper I will describe short- and long-term population fluctuations of Hawk Owls in Fennoscandia by reviewing the literature and presenting personal data, identify factors associated with these fluctuations, evaluate whether modern forestry, which emphasizes clear-cut harvesting, creates a habitat where Hawk Owls hunt more efficiently compared to old forest and suggest strategies that would improve clear-cuts as foraging habitat for Hawk Owls.

METHODS

In a 50 km² (4 km × 12.5 km) area in the boreal forest at 550–750 m elevation in southeastern Norway (61°N, 11°E) the annual number of breeding Hawk Owls were recorded during 1971–95. Each year, all nest boxes and known natural cavities were checked at least once to reveal nesting attempts by Hawk Owls and Tengmalm's Owls (*Aegolius funereus funereus*). Further information on

the area and the nest-visit procedure is given by Sonerud (1985, 1986).

Information on microtine abundance was obtained from observations made when checking nest boxes and from snap-trapping in a permanently established trap line system at the southern end (60°56'N, 11°08'E) of the Hawk Owl nesting area since 1977. This system covers about 40 ha in a clear-cut and the surrounding old forest stands, as described by Sonerud (1986, 1988). During spring (mid- or late-May) in 1977–78 and 1981–95, summer (late July or early August) in 1977 and 1981–90 and fall (late September or early October) in 1977 and 1981–95, about 300 traps (type "Rapp") baited with stained cocoa fat were put out 5 m apart in seven separate lines and checked on each of the following four days (Sonerud 1986, 1988).

In the same clear-cut as microtines were snap-trapped, I also recorded Hawk Owl foraging behavior during 1976–92. The clear-cut covers 20 ha (800 m × 250 m) and contains an average mix of the dominant boreal forest types in Fennoscandia. Before I started recording Hawk Owl foraging behavior, I experimentally modified the clear-cut. First, I removed all trees and snags remaining after logging, except 10 mature Scotch pines (*Pinus sylvestris*). I then divided the clear-cut into eight squares, and within four of these a total of 178 artificial poles with a top-mounted perch were erected. The poles were of three different heights, providing perches 1.5 m (61 poles), 3.0 m (59 poles) and 6.0 m (58 poles) above ground. Within each square, the poles were spaced 20 m apart in a grid. The positions of the different heights were assigned randomly. On the borders between the squares another 23 poles with a top-mounted nest box for owls with a perch height of 4.5 m were erected 40 m apart and 14 m from the nearest adjacent pole. The pines varied in height from 13–20 m, and were within two of the squares containing poles. Thus a total of 211 perches with heights from 1.5–20 m were provided on approximately half the area of the clear-cut.

In this clear-cut, I recorded the foraging behavior of 10 Hawk Owls (Table 1). These were the only ones available for observation, as Hawk Owls are not resident over a longer time in any part of their range. The behavior of the owls was observed from a permanent blind on a hill in the middle of the clear-cut using 7× or 10× binoculars and a 25–40× spotting scope and recorded by the focal-animal method (Altmann 1974). The owls were observed at all times of the day and as long as they remained foraging within the clear-cut. In most cases only one owl was foraging in the clear-cut at a time. The exceptions were nesting pairs. If both mates were available for observation, I always observed the male (Sonerud 1992).

The Hawk Owls always searched for prey by perching. Hovering was employed only as an interruption of an attack upon prey and generally for a few seconds only. The owls were never observed to attack prey while flying between perches. They abandoned perches either to move to another perch or to attack prey. I only recorded perch records of the latter type, which were made when the ground was snow free and for which the perch height and the corresponding horizontal attack distance were known. This sample included 246 attacks (Table 1).

The heights of perches other than poles were estimat-

Table 1. Individual characteristics, sample period and sample size used in this study, of 10 Hawk Owls observed in an experimentally modified clear-cut. Attack records included were those made on snow-free ground and for which both the horizontal attack distance and the height of the perch from which the attack was launched were known.

IND.	SEX	PROVIDING MATE OR NEST-LINGS	SAMPLING PERIOD	NUMBER OF ATTACK RECORDS
1	Male	No	28 Sept.–3 Oct. 1976	2
2	Unknown	Yes	26–28 June 1977	36
3	Unknown	No	1 Sept. 1977	2
4	Male	Yes	26 April–11 June 1981	69
5	Unknown	No	1–30 Oct. 1983	17
6	Male	Yes	20 April–3 June 1984	22
7	Female	Yes	7–22 June 1984	39
8	Female	No	26 Aug.–6 Nov. 1984	11
9	Male	Yes	14 May–16 June 1985	44
10	Unknown	No	29 Sept.–1 Oct. 1992	4

ed by using a clinometer. Horizontal attack distances were either paced or calculated from the map of the grids, while those outside the grids were paced. Some of the long attack distances (>50 m) were measured on a specially made aerial orthophoto of the study area (area-correct scale 1:5000). Flight time elapsed from launching an attack to capturing (or missing) prey was recorded by using a stopwatch. Horizontal attack distances that I was unable to measure, but for which the corresponding flight time had been recorded, were estimated from the perching height and the real attack distance; the latter was in these cases estimated from a linear equation between flight time and real attack distance calculated for each individual.

POPULATION TRENDS

Hawk Owls in the western Palearctic are thought to fluctuate in synchrony with their microtine prey (Cramp 1985). In my study area Hawk Owls were found nesting in only seven of the 25 yr from 1971–1995 (Fig. 1). These 7 yr were all within the 12-yr period 1977–88. All nestings occurred when microtine density was increasing or in peak years, although Hawk Owls were not present in all such years (Fig. 1). Hawk Owls were observed outside the nesting season here in an additional 5 yr (1976, 1982, 1983, 1989 and 1992).

In an area in western Finland (63°N, 23°E), Hawk Owls nested in only 5 of the 14 yr from 1979–90 and only when microtines were abundant.

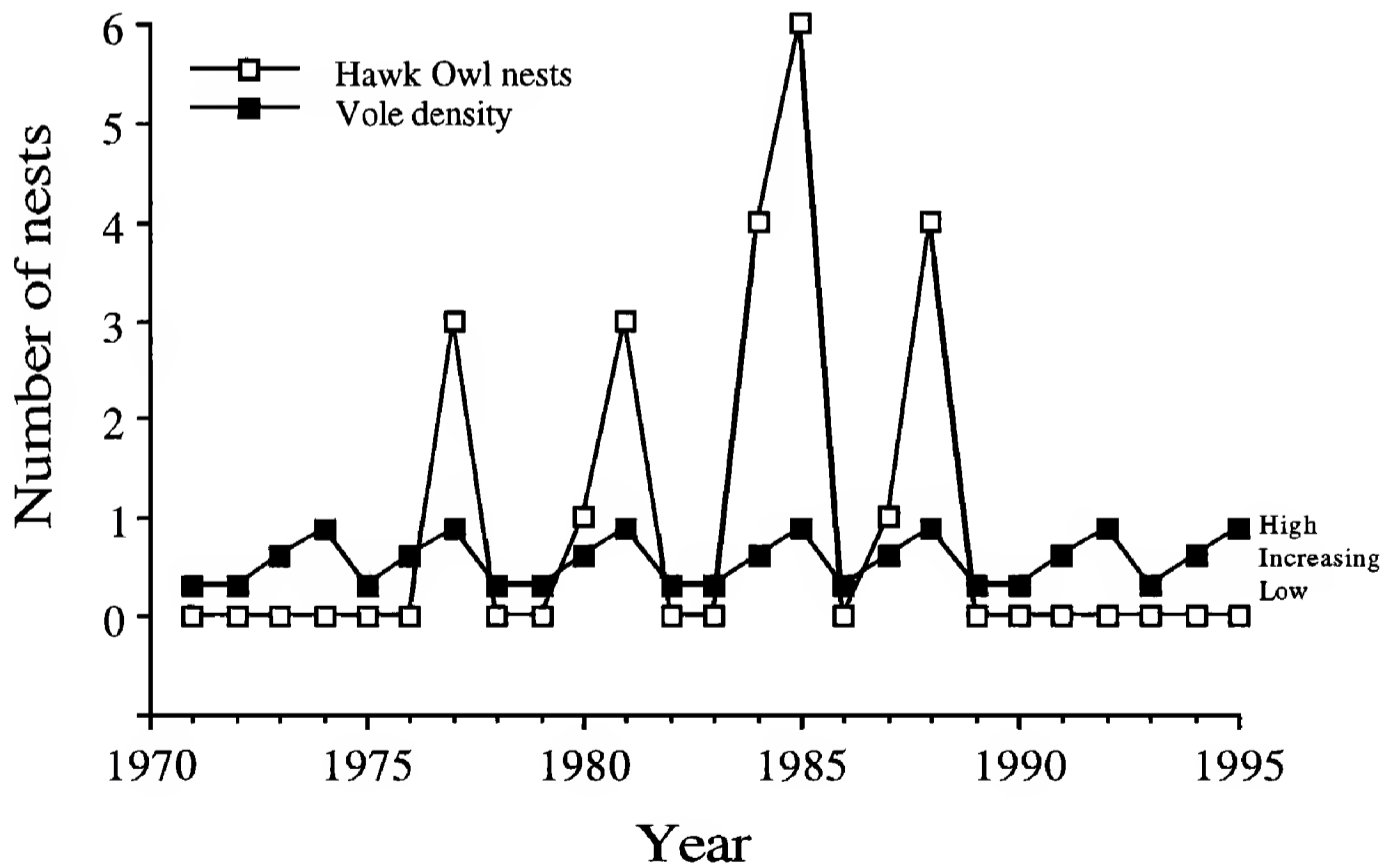


Figure 1. The number of recorded Hawk Owl nests and the population density of microtines in a 50 km² study area in the northern boreal zone in southeastern Norway during 1971–95. The microtine density is scored as low, increasing and high.

Hawk Owls held winter territories here in an additional 3 yr (Korpimäki 1994).

In Fennoscandia, population densities of microtines fluctuate widely, usually with peaks every 3–4 yr (Fig. 1, Hansson and Henttonen 1985). These microtine population fluctuations are geographically asynchronous (Hagen 1956, Myrberget 1965, Myllymäki et al. 1977, Christiansen 1983), even over a scale of less than 100 km (Steen et al. 1996). Because Hawk Owls seem to depend on high microtine densities for nesting (Fig. 1, Korpimäki 1994), the large temporal and spatial variations in microtine densities in Fennoscandia probably select for Hawk Owls with high capabilities of tracking microtine populations. Although the nomadic life of Hawk Owls is accepted as fact (Mikkola 1983, Cramp 1985), documentation is limited to records of invasions (Hagen 1956, Byrkjedal and Langhelle 1986) and scattered ringing (banding) recoveries. Hawk Owls ringed as nestlings in Fennoscandia have dispersed up to 1900 km in all directions, including east into Russia (Glutz von Blotzheim and Bauer 1980, Cramp 1985, Sonerud 1994). Recoveries of Hawk Owls ringed as breeding adults include examples of both males and females residing in an area from one nesting season to the next when microtine abundance remained high and of both sexes leaving when microtine populations declined. There are no examples of Hawk Owls residing in an area from one microtine peak to the next (Sonerud 1994).

In Fennoscandia the number of Hawk Owls at any time is determined largely by the arrival of nomadic owls from Russia and the level of local reproductive output. In this century, large populations were noted in the fall of 1912, 1950 and 1983 (Hagen 1952, 1956, Edberg 1955, Byrkjedal and Langhelle 1986, Risberg 1990). The relative roles of immigration and local reproduction will vary between Hawk Owl population peaks because these factors are determined by the current microtine rodent population phase in Russia and Fennoscandia, respectively. The unprecedented population peak in 1983 seemed to mostly include owls from outside Fennoscandia (Mikkola 1983, Byrkjedal and Langhelle 1986). The dispute about the origin of the Hawk Owls which made up the large population in the southern parts of Fennoscandia in fall 1950 (Edberg 1955, Hagen 1956), however, illustrates the difficulty in determining the relative importance of immigration and local reproduction

for the current size of the Fennoscandian Hawk Owl population.

The number of breeding Hawk Owls in Fennoscandia seems to have peaked in years when immigration from the east during the preceding fall occurred when the local microtine population was increasing toward a peak. The highest recorded number of breeding Hawk Owls in the central and southern parts of Norway and Sweden occurred in the microtine peak years 1984 and 1985, after the unprecedented immigration of Hawk Owls in fall 1983 (Byrkjedal and Langhelle 1986, Risberg 1990). This influx occurred at a time when the local microtine populations were increasing (Sonerud 1988, Lindström and Hörnfeldt 1994). Similarly, a rather large influx of Hawk Owls into Finland from Russia in fall 1957 coincided with a microtine peak in Finland and many owls stayed to breed there in 1958 (Mikkola 1983).

The total number of Hawk Owls present in Fennoscandia at any time may vary over two orders of magnitude, from a few hundred up to tens of thousands. The temporal and spatial variation in Hawk Owl population density in Fennoscandia makes an estimate of the total population difficult. The numbers of Hawk Owls during peak years have been estimated at 3600 pairs in Finland (Merikallio 1958, cited in Cramp 1985), 10 000 pairs in Sweden (Ulfstrand and Högstedt 1976) and 10 000 pairs in Norway (Sonerud 1994).

Information on long-term population changes of Hawk Owls is sparse, especially from the northern parts of Fennoscandia where Hawk Owls occur more commonly and regularly than in the southern parts (Haftorn 1971, Hyttiä et al. 1983, Risberg 1990), but where few people live. In southern and central parts of Norway and Sweden the Hawk Owl has been more common in the last 25 yr, especially during the period 1975–1989, than in the preceding 25 yr (Risberg 1990, Sonerud 1994). In Finland, the Hawk Owl was thought to have declined from the 19th century until the 1950s (Merikallio 1958, cited in Cramp 1985). In southern Norway, Hawk Owls were less frequent during 1914–1948 than during 1880–1913; in fact none were recorded nesting here between 1913 and 1949 (Hagen 1952). In conclusion, the Hawk Owl seems to have been more common in Fennoscandia during the first and last quarters of the past 100 yr than in the intervening time.

FACTORS ASSOCIATED WITH FLUCTUATIONS IN HAWK OWL NUMBERS

One explanation for the decline in the number of breeding Hawk Owls in Finland from the 19th century until the 1950s was thought to be human persecution (Merikallio 1958, cited in Cramp 1985). Hawk Owls are easy targets because they are diurnal, use exposed perches and are relatively tame. Earlier in this century Hawk Owls were often shot in years of population peaks in Norway (Hagen 1952). Nowadays, Hawk Owls are protected by law in Fennoscandia and fewer are killed.

Hawk Owls usually nest on top of broken trees, in cavities made by the Black Woodpecker (*Dryocopus martius*), in nest boxes and sometimes in nests made by corvids (Cramp 1985, Sonerud 1985). Since modern forests contain fewer trees old enough to provide cavities suitable as nesting sites for Hawk Owls, the breeding opportunities of Hawk Owls might locally be limited where the forest has been intensively managed. One reason for the decline in the number of breeding Hawk Owls in Finland from the 19th century until the 1950s was thought to be the disappearance of hollow trees (Merikallio 1958, cited in Cramp 1985).

Two factors appear to explain why Hawk Owls have been more common in the central and southern parts of Norway and Sweden during the past 25 yr. The first is the occurrence of a moderate invasion in fall 1975 and a large invasion in fall 1983 (Risberg 1990). The second factor is probably the opening of the forest by clear-cutting that has taken place the past 30–40 yr. This has made larger areas of the forest suitable for the Hawk Owl (Norberg 1987). In addition, clear-cuts support greater populations of microtines than does old forest (Henttonen et al. 1977, Larsson and Hansson 1977, Hansson 1978).

HOW SHOULD CLEAR-CUTS BE DESIGNED TO SUIT HAWK OWLS?

Harvesting old forest by clear-cutting may benefit the Hawk Owl by creating habitats that are more profitable for hunting than the natural or the selectively cut old forest. Due to its dependence on vision for locating prey, the Hawk Owl is capable of using open forest with ample space for long range scanning of and attack at ground-dwelling small mammals (Norberg 1987). However, due to the Hawk Owl's dependence on elevated perches from which it searches for prey (Sonerud 1980), clear-cuts may not offer suitable types and densities

of hunting perches. In the experimentally modified clear-cut (see Methods), the four blocks provided with perches were utilized more for hunting by Hawk Owls, Common Buzzards (*Buteo buteo*) and European Kestrels (*Falco tinnunculus*) than the four blocks without perches (Sonerud 1980). In Sweden, clear-cuts experimentally provided with perches were utilized more by Common Buzzards than clear-cuts without perches (Widén 1994). By knowing the size of the Hawk Owl's search range from hunting perches, it may be possible to calculate an optimal interperch distance and to design clear-cuts where Hawk Owls can forage effectively.

Size of Clear-cuts. To know how wide clear-cuts lacking residual trees may be without being inaccessible to Hawk Owls, I estimated how far into a clear-cut a Hawk Owl's search range extends from a perch in the forest edge. An appropriate estimate of the search range may be the distance containing all recorded attack distances or all but the most extreme ones (90th percentile). Use of the latter is justified because very long attack distances may be traveled under special conditions, and because successful attacks tended to be made at shorter distances than unsuccessful ones when the ground was snow free (Sonerud 1992). From perches ≥ 9 m above the ground, as typically found at the edges of clear-cuts, the estimated search range of the Hawk Owls in the experimental clear-cut would be about 70 m if taken as the 90th percentile and 110 m if taken as the longest of the recorded attack distances from such perches on snow-free ground ($N = 29$). Thus, even if clear-cuts are 140 m wide, Hawk Owls hunting from perches in the remaining forest seem able to utilize all the area for hunting in the snow-free season.

Shapes of Clear-cuts. The results above suggest that square-shaped clear-cuts up to about 2 ha in size may be accessible for Hawk Owls from perches at the forest edge. Rectangular clear-cuts of all sizes may be accessible from the edge provided the short side does not exceed 140 m. If no residual trees remain in a clear-cut after logging so that Hawk Owls are left only with the perches made up by the forest edge, larger parts of the clear-cut will be available to Hawk Owls as the edge-area ratio becomes larger. Thus, complex clear-cuts with convoluted edges may be more beneficial to Hawk Owls than simple clear-cuts with linear edges.

Residual Trees. The results above suggest that if clear-cuts are made wider than 140 m and no re-

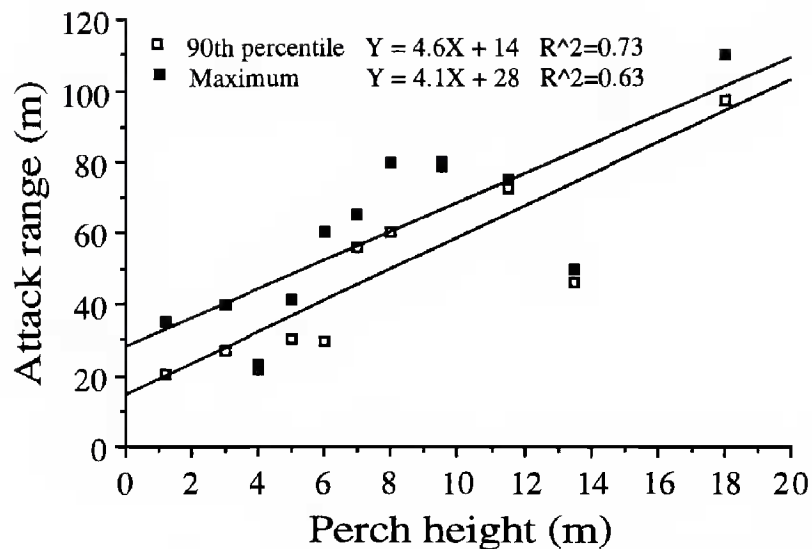


Figure 2. Search range of Hawk Owls in relation to perch height, estimated as the 90th percentile and the longest of the recorded horizontal attack distances, respectively.

sidual trees are left, the central areas >70 m from the edge may be inaccessible to Hawk Owls. Therefore, stumps, snags and other trees of little economic value should be left as hunting perches for Hawk Owls. If such residuals are provided, there may be no upper size limit on clear-cuts that may be utilized by Hawk Owls, unless the Hawk Owl's vulnerability to other raptors increases in large clear-cuts. Most documented Hawk Owl kills in Fennoscandia are made by Eagle Owls (*Bubo bubo*), which also hunt in open habitats (Mikkola 1983).

An important issue is to estimate how far apart the residual trees in a clear-cut may be spaced without making some of the clear-cut inaccessible to Hawk Owls. If we assume that the search area from a single perch is confined within a circle around that perch (Andersson 1981) and that all parts of the clear-cut are to be covered by the search areas from the perches there, then the longest acceptable interperch distance for perches of a certain height is the estimated search range from that height multiplied with $\sqrt{2}$.

When the ground was snow free, the horizontal attack distance of the Hawk Owls foraging in the experimental clear-cut increased with the height of the perch from which the attack was launched (Sonerud 1992). I therefore estimated the search range, both as the 90th percentile and as the maximum of the recorded horizontal attack distances for different perch heights (Fig. 2). Perches of similar height were combined in some cases to obtain sufficiently large samples. These estimates of the search range increase with increasing perch height (Fig. 2).

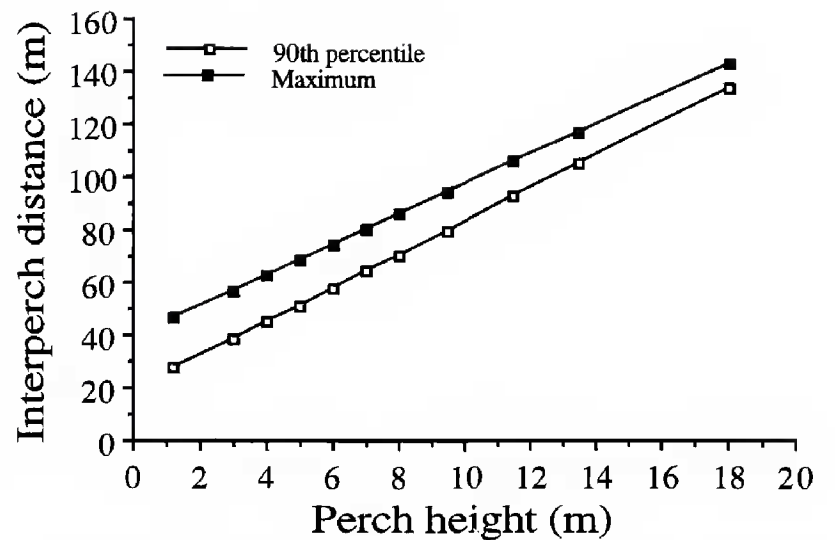


Figure 3. Maximum acceptable distance between residual trees, left as hunting perches for Hawk Owls in clear-cuts, as a function of their height. The values are taken as the search range values given by the regression line in Fig. 2 multiplied with $\sqrt{2}$.

To obtain a simplified picture of the Hawk Owl's search range as a function of perch height, I regressed the search range estimates for each group of perch heights on the average perch height of the actual group (Fig. 2). Thereafter, I calculated the longest acceptable interperch distances by multiplying the search range values as given by the regression line with $\sqrt{2}$ (Fig. 3). If the search range is taken as the 90th percentile of the recorded attack distances, the maximum acceptable interperch distance increases from about 30 m for residuals ≤ 3 m high to about 130 m for residuals ≥ 15 m high (Fig. 3). Thus, an array of residuals should be left with a density varying from ≥ 14 per ha for the shortest ones to ≥ 0.6 per ha for the tallest ones. If the search range from a certain perch height is taken as the longest recorded attack distance from that height, the maximum interperch distance increases from about 50 m for residuals ≤ 3 m high to about 140 m for residuals ≥ 15 m high (Fig. 3). Thus, an array of residuals should be left with density varying from ≥ 5 per ha for the shortest ones to ≥ 0.5 per ha for the tallest ones.

Because these estimates are based on data from one clear-cut only, forest managers should use flexible strategies for the spacing of residuals. As a rule of thumb, I would suggest that in parts of clear-cuts >100 m from the forest edge residuals should include about 1 per ha for tall (>15 m) residuals, and about 10 per ha for short (<3 m) residuals.

Effect of Seasonal Change in Vegetation Height. When I estimated the Hawk Owl's search range

above, I disregarded any seasonal change in the cover for voles provided by the field vegetation. However, a Hawk Owl's view of voles moving along the ground would be expected to be more obstructed in late summer and fall than in spring just after the snow has disappeared and before the vegetation has leafed out (Jacobsen and Sonerud 1993). Thus, the maximum acceptable interperch distance, as estimated above based on data from the whole snow-free season, may be too long in late summer and fall.

Effect of Snow Cover. Hawk Owls live in areas where the ground may be snow covered for half the year or more. Because they rely on sight to locate prey, Hawk Owls nearly always attack prey exposed on top of the snow (Sonerud 1986, Nybo and Sonerud 1990). Voles are more visible when moving on top of the snow than when moving in the vegetation. In fact, the Hawk Owl's search range is longer for prey moving on top of the snow than for prey moving on snow-free ground (Sonerud 1980, 1992). Thus, the maximum acceptable interperch distance, as estimated above based on data from the snow-free season, would allow Hawk Owls access to all parts of a clear-cut in winter as well.

OPTIMAL HABITAT OF HAWK OWLS IN MODERN FORESTS

Hawk Owls usually switch their diet from mostly bank voles (*Clethrionomys glareolus*) to mostly *Microtus* voles as snow disappears in spring, probably because bank voles move on top of the snow cover more frequently than do *Microtus* voles (Sonerud 1986, Nybo and Sonerud 1990, Jacobsen and Sonerud 1993). In Fennoscandia, *Microtus* voles are almost exclusively found in clear-cuts, whereas *Clethrionomys* voles, especially the bank vole, occur in a wide range of habitats but more commonly in forest than in clear-cuts, especially during spring (Henttonen et al. 1977, Larsson and Hansson 1977, Hansson 1978, Sonerud 1986). Thus, variation in diet suggests that Hawk Owls switch major hunting habitat from forests to clear-cuts as snow disappears and that Hawk Owls may find best foraging opportunities in forest habitats during the winter, provided the forest is open enough to allow the Hawk Owl to take full advantage of its long search range on snow.

In Fennoscandia, the overall density of voles is usually higher in clear-cuts than in forest, primarily because *Microtus* voles reach higher densities than *Clethrionomys* voles (Henttonen 1989). Except just after snow melt and before the vegetation leafs out,

vegetation cover is on average more luxurious and offers more protection for voles in clear-cuts than in forest (Sonerud et al. 1986). Hence, for Hawk Owls prey availability is greater in clear-cuts than in forest only from just after snow melt until the new vegetation leafs out; thereafter the relative prey availability in clear-cuts compared to forest declines (Jacobsen and Sonerud 1993). When snow starts accumulating, prey availability soon becomes higher in forest than in clear-cuts. Thus, the relative prey availability in clear-cuts compared to forest is lowest when snow covers the ground, highest just after snow melt and declines gradually throughout the snow-free season.

Because neither forest nor clear-cuts can serve as the best foraging habitat for Hawk Owls throughout the year in Fennoscandia, the optimal forest landscape for Hawk Owls would be a mix of old forest and clear-cuts. The area ratio between these two main habitat types that maximizes the Hawk Owl's intake rate cannot be determined at present because the change in relative prey availability in each habitat throughout the year is not sufficiently known. However, if clear-cut areas too large to be covered by the Hawk Owl's attack range from the forest edge are left with a sufficiently dense array of snags, stumps and other residuals after logging, and if trees with potential nesting cavities for Hawk Owls are left after logging, the species may benefit from modern forestry.

The Hawk Owl is unlikely to show any evolutionary response to modern forestry or other logging operations by man in Fennoscandia because any genetic effect is probably swamped by the long dispersal undertaken by young and old birds of both sexes. Therefore, Hawk Owls in Fennoscandia are mainly adapted to the forest habitats in Siberia, which probably have been shaped mainly by fires until recently.

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